NeuroImage 45 (2009) 587–597

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

Connectivity and signal intensity in the parieto-occipital cortex predicts top-down attentional effect in visual masking: An fMRI study based on individual differences ☆

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ARTICLE INFO

Article history:
Received 4 August 2008
Revised 30 October 2008
Accepted 17 November 2008
Available online 6 December 2008

Keywords:
Attention
Vision
Structural equation modeling
Connectivity
Individual difference
Intraparietal sulcus
Functional MRI

ABSTRACT

Top-down attention affects even the early stages of visual processing. For example, several studies have reported that instructions prior to the presentation of visual stimuli can both enhance and reduce visual masking. The finding that top-down processing influences perceptual processing is called the attentional effect. However, the magnitude of the attentional effect differs between individuals, and how these differences relate to brain activation remains to be explained. One possibility would be that activation intensity predicts the magnitude of the attentional effect. Another possible explanation would be that effective connectivity among activated areas determines the attentional effect. In the present study, we used structural equation modeling to analyze individual differences in the attentional effect on visual masking, in relation to the signal and connectivity strength of activated brain regions prior to presentation of the visual stimuli. The results showed that signal intensity was positively correlated with attentional effect in the occipital areas, but not in fronto-parietal areas, and the effect was also positively correlated with connective efficiency from the right intraparietal sulcus (IPS) to the bilateral fusiform gyrus (GF). Furthermore, a higher degree of effective connections from the right IPS to the GF led to greater neural activity in the GF. We therefore propose that the effective modulator in the parietal areas and strong activation in the visual areas together and in cooperation predict higher attentional effects in visual processing.

Introduction

Our eyes continuously receive a large amount of visual information, but the capacity-limited brain can process only a fraction of this information (Tsotsos, 1990; Lennie, 2003). Therefore, we have an attentional mechanism to select information that is relevant to our current behavioral goals. Recent psychophysical studies have shown that top-down selective attention functions even during the early stages of visual processing. One typical case is metacontrast masking, where the visibility of a target stimulus decreases due to a subsequent masking stimulus (Breitmeyer, 1984). Metacontrast masking has been thought to occur at the early perceptual stages, because it is influenced by elementary stimulus dimensions such as spatial frequency and color (Williams et al., 1991). However, Ramachandran and Cobb (1995) showed that, using the exact same stimulus presentation, instructions presented prior to the visual stimuli strongly modulate this masking effect. In their experiment, when participants were instructed to attend the target, the masking effect was reduced, whereas, when they were instructed to attend the mask, the masking effect was enhanced (see also Shelley-Tremblay and Mack, 1999; Boyer and Ro, 2007). The general finding that top-down processing influences perceptual processing is called the attentional effect. Interestingly, the magnitude of the attentional effect in visual experiments differs between individuals, and these differences are thought to be due to variations in the capacity to efficiently differentiate between relevant and irrelevant information (Lansman et al., 1983; Ress et al., 2000; Silver et al., 2005; Giesbrecht et al., 2006).

Previous neuroimaging studies with positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have investigated the neural substrates of top-down attention. These

☆ Funding: This work was supported in part by grants from the Research Fellowships of the Japan Society for the Promotion of Science for Young Scientists 04J00473 to H.T.; Japan Society for the Promotion of the Science Grant 20019041 and 20033030 to T.H. and 19203032 and 19653082 to N.O.; Ministry of Education, Culture, Sports, Science, and Technology of Japan Grants-in-Aid for Scientific Research on Priority Areas (Integrative Brain Research) 20020013 to H.F.; and a grant from New Energy and Industrial Technology Development, Japan 51101244-0 to H.F.
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1053-8119/$ – see front matter
doi:10.1016/j.neuroimage.2008.11.028

studies have suggested that directing attention to the spatial location of a visual stimulus increases stimulus-evoked activity in the corresponding occipital areas (Tootell et al., 1998; Brefczynski and DeYoe, 1999; Martinez et al., 1999, 2001). Moreover, attention increases baseline activity in the occipital cortex even before the presentation of a visual stimulus (Kastner et al., 1999; Hopfinger et al., 2000; Giesbrecht et al., 2003; Weissman et al., 2004; Woldorff et al., 2004). In addition to the occipital areas, attention is also associated with activation in fronto-parietal areas (Corbetta et al., 1993, 1998; Hanakawa et al., 2002). Fronto-parietal areas appear to be activated earlier (Hopf et al., 2000; Brass et al., 2005; Grent-'t-Jong and Woldorff, 2007) and more strongly (Kastner et al., 1999) than occipital areas, suggesting that fronto-parietal areas could modulate neural activity in the occipital areas. Recent studies using a combination of transcranial magnetic stimulation and positron emission tomography (TMS-PET) or transcranial magnetic stimulation and event-related potential (TMS-ERP) confirmed causal relationships amongst patterns of cortical activity in these areas. Applying TMS to the frontal eye field, which is one of the key sites in the fronto-parietal network, clearly affects neural activity in the parietal (Paus et al., 1997) and occipital cortices (Paus et al., 1997; Ruff et al., 2006; Taylor et al., 2007).

Increases in pre-stimulus activity in the visual cortex have been thought to relate to how the brain prepares to process an expected stimulus in the attended location (Kastner and Ungerleider, 2000). Consistent with this conjecture, several studies have reported that the intensity of pre-stimulus activity in the occipital cortex predicts attentional effects on both visual detection and discrimination tasks (Ress et al., 2000; Müller et al., 2003; Serences et al., 2004; Sapir et al., 2005; Giesbrecht et al., 2006). Unfortunately, it remains unclear how the fronto-parietal areas are involved in the attentional effect, as these studies limited their analyses to the occipital cortex.

To fully understand the neural substrates of top-down attention, it would be necessary to clarify how both the fronto-parietal and occipital areas are involved in the attentional effect. One hypothesis (in line with the research presented above) would be that the intensity of the fronto-parietal activation predicts the attentional effect, in the same way that activation in the occipital areas predicts the effect (we call this “the signal intensity hypothesis” in the present study). Indeed, recent studies have provided findings supporting the signal intensity hypothesis, showing that preparatory activity in the fronto-parietal cortex predicts the reaction-time performance in higher-order cognitive tasks (Weissman et al., 2006; Stern et al., 2007). However, several other studies suggest that effective connectivity between activated brain areas plays an important role in modifying behavior, such as behavioral performance in working memory tasks (Glabus et al., 2003; Kondo et al., 2004a,b) and associative learning tasks (McIntosh et al., 1998, Büchel and Friston, 1997). Given the possibility that the fronto-parietal areas modulate activation in the occipital areas, a second hypothesis would be that effective connectivity within the fronto-parietal areas or between fronto-parietal and occipital areas predicts the attentional effect (we call this “the effective connectivity hypothesis” in the present study). These two hypotheses could both be valid: which one is more appropriate may depend on the cortical region. Furthermore, if these two hypotheses were simultaneously valid, another interesting investigation would focus on the relationships of these two different aspects of neural activity. For example, it would be possible that an efficient connection induces strong activation in some areas.

To investigate these issues, we used fMRI to explore the neural substrates of attentional effect at the whole-brain level, employing the same experimental paradigm as Ramachandran and Cobb (1995). The task for participants was to identify and report the level of visibility for a briefly presented visual target that was followed by a number of masks. Before visual presentation, we instructed participants to pay attention to the target, the masks or neither. We observed how the masking effect changed depending on the instructions given. Using SEM (or structural equation modeling, see Büchel and Friston, 1997; Horwitz et al., 1999), we then analyzed how individual differences in the magnitude of the attentional effect correlated with signal intensity as well as effective connectivity. This experimental paradigm was suitable for studying the neural substrates of the attentional effect, as it allowed us to track individual differences in the attentional effect under identical stimulus presentation conditions.

Methods

Participants

Eight (5 male and 3 female; age range = 21–26 years) and 10 (7 male and 3 female; age range = 22–27 years) university students participated in the preliminary behavioral experiment and in the fMRI experiment, respectively. All participants were naive to the purpose of the study, were right-handed as assessed by the Oldfield handedness questionnaire (Oldfield, 1971), and reported normal or corrected-to-normal vision. None of the participants had a previous history of neurological or psychiatric disorders. All participants gave written informed consent. The experiment was conducted in accordance with the ethical guidelines of the Declaration of Helsinki and approved by the Committee of Medical Ethics, Graduate School of Medicine, Kyoto University.

Behavioral procedure

Preliminary behavioral experiment

To investigate the psychophysical profile of how top-down spatial attention modulates metacontrast masking, we conducted a preliminary behavioral experiment based on the study by Ramachandran and Cobb (1995).

The experiment was controlled by Presentation software (Neurobehavioral Systems Inc., San Francisco, CA, USA). Stimuli were presented on a video monitor viewed at a distance of 57 cm. Fig. 1 shows a schematic diagram of the experiment. Each stimulus subtended $1° \times 1°$ and was presented in gray (0.54 cd/m^2) against a

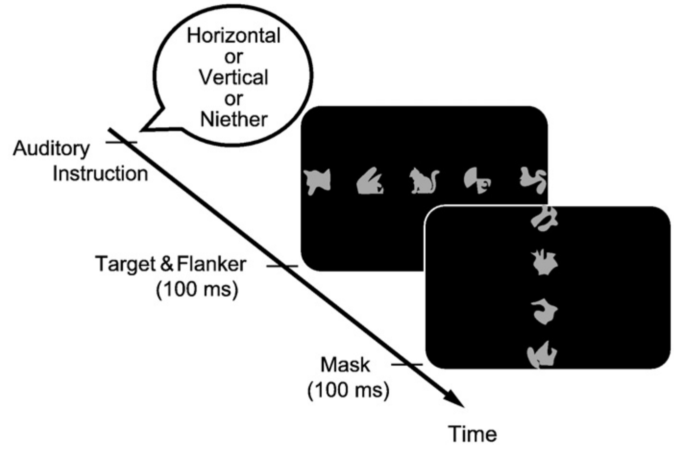

Fig. 1. Event sequence of the trials. At the beginning of the trials, an auditory instruction prompted participants to prepare to attend the horizontal row, vertical column, or neither of the two. A target was displayed on the center accompanying two flankers in the horizontal row. Masks in the vertical column followed the target with SOA of 0, 100 or 300 ms. After the stimulus sequence, participants rated the subjective visibility of the target on a 6-point scale (1, invisible to 6, clearly visible), and reported the target identity aloud. In the fMRI experiment, the following points were changed; SOA between the auditory instructions and target display was 8 or 8.5 s, sufficient to observe pre-stimulus brain activity. SOA between the horizontal row and the vertical column was fixed at 100 ms. Participants did not need to report the target identity.